# Middle Temporal Cortical Visual Area Visuospatial Function in *Galago senegalensis*

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Wilson, M., Keys, W., & Johnston, T. D. 1979 "Middle temporal cortical visual area and visuospatial function in Galago senegalensis" Journal of Comparative and Physiological Psychology 92:247-259.



## Abstract:

Bushbabies with lesions restricted to the middle temporal (MT) area and animals with larger extrastriate lesions including area MT were compared with normal control animals on tests of visuospatial localization and discrimination learning. Ablation of area MT was sufficient to produce impairments in directing behavior appropriately on the basis of visuospatial cues. Extension of the lesion into areas 18 and 19 produced more profound deficits. Retardation in learning a stripe discrimination problem was correlated with the extent of damage to the geniculostriate system. It is hypothesized that area MT is important in achieving and maintaining fixation on a target whereas cortical areas 18 and 19 are necessary for establishing the location of stimulation in visual space.

## Article:

The data reported here provide further evidence on the role of the middle temporal (MT) area in visuospatial function. An area that may be homologous has been identified by anatomical and electrophysiological methods in a number of primate species (Allman & Kaas, 1971; Allman, Kaas, & Lane, 1973; Doty, Kimura, & Mogenson, 1964; Glendenning, Hall, Diamond, & Hall, 1975; Zeki, 1974). However, its role in visually guided behavior has only recently been studied in the bushbaby *(Galago senegalensis;* Wilson, Diamond, Ravizza, & Glendenning, 1975) and in the rhesus monkey (Wilson, Wilson, & Remez, 1977). The bushbaby is a useful species for such studies because the thalamocortical projections to MT and other cortical visual areas are known and, from present evidence, appear to be nonoverlapping, That is to say, the MT area is the cortical target of fibers from the tectorecipient portion of the inferior pulvinar nucleus of the thalamus, and extrastriate areas posterior and ventral to MT receive input from the superior portion of the pulvinar (Glendenning et al., 1975). Sole input to this latter portion of the pulvinar appears to be from cortical visual areas and other thalamic nuclei (Raczkowski & Diamond, 1976). Thus area MT receives direct input from the retina, via the superficial layers of the superior colliculus and the inferior pulvinar, whereas areas 18 and 19 and ventral temporal cortex receive indirect retinal input through a cortico-thalamo-cortical circuit.

In a previous behavioral study of MT function in the bushbaby, lesions of this area, but not of ventral temporal cortex, consistently impaired the ability of animals to utilize relevant cues in space, i.e., to make use of a visual "landmark" to guide responses appropriately (Wilson et al., 1975). The results of that experiment did not permit an unambiguous interpretation of the deficit since the landmark, although its location varied, always appeared in the upper visual field. It was not clear whether the animals that were impaired failed to search portions of visual space or whether visual search was normal and the animals were unable to learn to make a response that was spatially discontiguous from the cue. It is also possible that they had a visual field deficit. In the present experiment a parametric study was undertaken to assess the ability of bushbabies with MT lesions or with larger lesions including prestriate cortex as well as area MT to locate visual information in space. This ability was

dissociated from the ability to make use of such information under conditions of varying degrees of separation from the response site. In addition, a pattern- discrimination learning task was presented which did not require locating a target since relevant information was available throughout the stimulus array. Finally, locating visual information was studied under two conditions of testing that required no associative learning and that approximated natural food-gathering activities of the animals.

## Method

### *Subjects*

Ten wild-horn bushbabies were used as subjects. They were untrained prior to the beginning of this experiment. Subjects were housed in individual wire mesh cages in a colony room, which permitted visual and auditory contact among animals. A 12-hr reversed day/night cycle was maintained throughout the study, and the temperature was kept constant at T8 °F. (25 °C). The animals were kept at 80%-90% of their ad lib weight on a diet of Purina Cat Chow and pureed fruit (Beech-Nut Baby Food). A vitamin-grease preparation was given once a week. Animal NC-8 died during postoperative testing. Another subject, Animal MT-2, became ill and was sacrificed before the experiment was completed. Data for these animals, when available, were included in the results.

### *Surgical and Histological Procedures*

Six animals were operated on, and four animals served as normal control (NC) animals. In some animals the intended lesion included only area MT, but in other animals, the extrastriate plus middle temporal (XS) group, larger lesions were imposed that included portions of areas 18 and 19 as well as area MT. All operations were bilateral and were done with sterile procedures while the animals were under deep sodium pentobarbital anesthesia. The animal was placed in a headholder, the skull was opened, and cortex was removed by aspiration with a fine-tipped glass sucker. Body temperature was monitored and was kept within normal limits with a heating pad. Upon completion of surgery, penicillin was administered im, and the animal was returned to its home cage where a period of at least 15 days was allowed for recovery.

When postoperative testing was completed, the animals were sacrificed with an overdose of sodium pentobarbital and were perfused intracardially with saline and formalin. The brains were embedded in celloidin and were sectioned in the frontal plane at 50 pm. Every 10th section through the brain and every 5th section through the lesion and the posterior thalamus were stained with thionine. Reconstructions of the lesions and drawings of the posterior thalamus were prepared from the sections.

### *Apparatus and Procedure*

*Visual discrimination.* For one set of tests, the bushbabies were trained preoperatively in a two-choice Yerkes apparatus. This has been described in detail elsewhere (Atencio, Diamond, & Ward, 1975) and was identical to that used in a previous investigation of MT function (Wilson et al., 1975). Briefly, it consisted of a black Plexiglas box with a clear top through which the animal could be viewed. A start box at one end of the apparatus was entered from the home cage through a sliding door. The animal left the start box through a guillotine door and entered the main area which was divided by a partition into two alleys. At the end of each alley, a swinging door could be pushed back to reveal a food well. The swinging doors consisfed of frames into which stimulus panels could be inserted. These were transilluminated by fluorescent light tubes mounted on the rear of the apparatus. The stimulus panels were square, 11 cm on a side. Stimuli were made by superimposing various commercially available patterns on white tracing paper. The stimuli were placed between sheets of clear Plexiglas, which were then taped together at the edges.

Before surgery, all the animals were accustomed to the discrimination apparatus and were required to learn to leave the start box and push one of the two stimulus panels without hesitation in order to obtain a live wax worm *(Galaria)* reward, At this point, a regimen of 30 trials per day, 5 days per week, was imposed, and a black—white discrimination was presented, with the black stimulus rewarded, The black stimulus appeared equally often on the left and right sides of the apparatus in a Gellermann sequence, To equalize olfactory cues, we baited both

food wells. The panel with the incorrect stimulus was kept locked during a trial. After making a response, and retrieving the reward on correct trials, the animal was returned to the start box.

After a subject reached a criterion of 9 correct in a block of 10 trials, the size of the black area on the positive stimulus was gradually reduced. First, an 8 X 8 cm black square on a white background was paired with the black, white negative stimulus. Following the subject's mastery of this problem to the same criterion, the size of the black square was reduced to 4 X 4 cm, and the animals were again trained to criterion, Then, black circles with diameters of 2.5 cm and 1.25 cm successively replaced the squares on the positive stimulus, and finally, at the end of the series, the animals were required to discriminate between a blank, white stimulus and a black circle, .64 cm in diameter, centered on a blank, white background. A barrier that divided the apparatus lengthwise into two alleys was introduced at each of the above stages of discrimination training, and a response was scored incorrect if the animal entered the alley leading to the negative stimulus, The length of the barrier was increased from 15 to 30 to 44.5 cm during each stage of training. On the last problem the animal was required to respond to the black circle when it represented 1° of visual arc, immediately after leaving the start box. In this final stage of preoperative training, criterion was set at 27 correct in a block of 30 trials.

After the operated animals recovered from surgery, all animals were retested on the final discrimination problem (blank plaque vs. .64-cm black circle on white background) which had been learned prior to surgery. If an animal was unable to relearn the discrimination, the length of the barrier and/or size of the cue was systematically varied, until a condition was found that produced successful performance. This was done in order to avoid confounding acuity deficits with an inability to locate the cue. When criterion was reached on this task, or on an easier version, as described in Results, formal testing was begun.

Three tests of visual function were presented in this apparatus. In the first test, the animal was again required to run down an alley to the stimulus panel that contained the small, black circle and to refrain from choosing the blank, white panel. Thirty trials/day were given in the same manner as preoperatively, with the positive stimulus appearing equally often on the left and right panels. However, on this test, the position of the cue varied between days, so on each testing day the animal had to locate the circle in a different place on the panel in order to make the appropriate response. The position of the cue was moved in a clockwise, spiral fashion from a position just above the center of the panel on Day 1 to the upper left hand corner on Day 20. The 20 possible positions of the cue are shown in Figure 1.

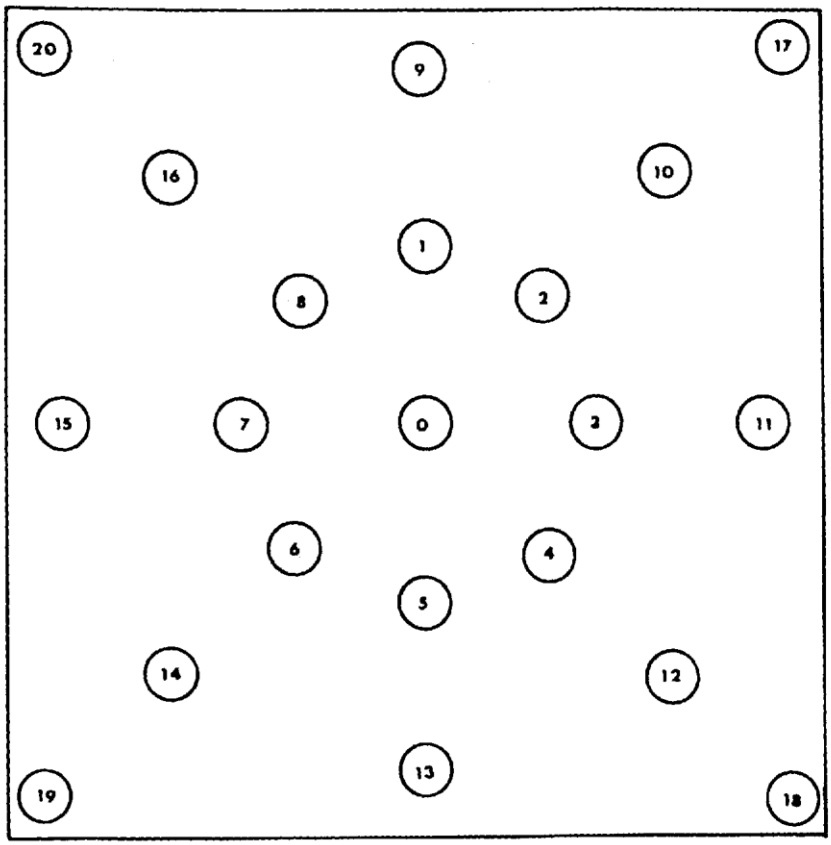



*Figure 1.* Twenty possible locations of cue in visual search tasks. (The circular cue subtended 1° of visual angle. On the stationary cue task, the cue appeared in the same position on all trials of a given day and appeared in the next higher numbered position on the subsequent day. On the variable cue task, the cue appeared in each of the possible positions once on each testing day.)

Before each testing session with the cue at a given location, the animal was retrained on the original problem, with the cue in the center (0) position. Trials were presented until five consecutive correct responses were made or until 30 trials had been given. If the animal was unable to achieve the warm-up criterion, it was returned to its home cage and tested in the same way on the next day. The warm-up trials accomplished two purposes. They ensured that the animal remembered which panel signaled reward, and they retrained the animal to look at the center of the stimulus panel at the beginning of each testing day.

The next test given was similar in procedure to the first test, but now the cue varied in location over all 20 positions within a single testing day. Testing was continued for 20 days, with 20 trials presented each day. The sequence of positions of the cue was varied in a Latin square design so that each cue location appeared once in a given spatial position within each day and was followed once by every other cue location over the 20- day sequence. Thus, temporal order effects, due to the spatial location of the cue on the previous trial, were balanced for all cue positions. On the second 10 days of testing, the barrier between the alleys was removed.

On the third test, the bushbabies were evaluated for their ability to learn a horizontal-vertical discrimination. The stimuli consisted of alternating black and white stripes, .64 cm in width, covering the entire stimulus panel. Choice of the panel with the horizontal stripes was rewarded. As in the first two tests, the animals were permitted to make a choice at the distance at which they could identify the .64-cm circle on warm-up tests, in order to control for differences in acuity which might have resulted from the lesions. Thirty trials/day were given until the animals reached a criterion of 27 correct in a block of 30 trials.

*Spatial localization.* Concurrently with discrimination training, the animals were trained to traverse a large, wire mesh tunnel, 3.66 m long. This task was modified from one described by Casagrande and Diamond (1974). The tunnel was divided into four compartments by .91 X .91 m plywood partitions. Each partition contained a

semicircular opening, 7.6 cm in diameter. In preoperative training, the openings were located at floor level in the middle of each partition. The animal entered a start box from its home box and was required to run through the tunnel to a goal box at the other end, where it received a wax worm reward. When the animal entered the start box and the goal box, a footplate connected to a Hunter digital timer was depressed, and the total number of seconds taken to run through the tunnel was automatically recorded. A Panasonic television camera was mounted on a table next to the tunnel. This was connected to a Sony television monitor in the adjoining room so that the animal's movements in the tunnel could he viewed and recorded on tape. Training in the tunnel took 1-2 wk. It was continued until the animal ran from the start box to the goal box in less than 5 min on each of five trials within a day.

After recovery from surgery, the animals were again trained in the tunnel, together with the normal control animals. Trials were continued until the animal ran through the tunnel in less than 60 see on each of the 5 trials within a day or until a total of 15 trials had been given.

Postoperatively, this part of the experiment tested the ability of the operated and normal animals to use visuospatial cues, by requiring the animals to find different pathways through the tunnel. On each of nisi 'r test days, the holes in the partitions were arranged curb that visual search and movement in the horizontal (lit, vertical ( V ), and combined horizontal and vertical ( H - V) planes were necessary to reach the goal box. Figure 5 shows the arrangement of the partitions lot typical pathways, and it can be seen that on the II pathways the animal never had to jump above the floor of the tunnel in order to traverse the holes but on the V and H-V pathways jumping and/or climbing was necessary. Depending on the arrangement of four different holes in the partitions, 12 different short (total length = 4.14 or 4.57 m) pathways and 6 different long (total length = 5.24 m) pathways were possible. This was done in order to determine whether the distance between holes was a critical factor in performance. A short and a long H, V, and H-V problem was presented on each testing day, making a total of six trials/day. The order in which the problems were given was counterbalanced within and between days. A failure was scored for an animal if it did not traverse the tunnel within 600 sec on a given pathway.

Prior to each day's trials, all animals were given warm-up trials on the straight horizontal pathway ' presented during postoperative retraining. lf an animal did not run through the tunnel as fast as it did during retraining, within six test trials, it was returned to its home cage and tested the next day.

*Ambient visual search.* The last task wasp resented postoperatively following the other tests, and it also investigated the ability to find a target in space. Live wax worms, which had been chilled in order to immobilize them and reduce odor cues, were placed at predetermined locations in a large enclosed arena. The arena consisted of wire mesh with steel supports and measured 122 X 61 X 61 cm. It was divided into two compartments, separated by a low barrier 1.75 cm high. Six wax worms were placed in the second compartment approximately 25 cm apart. A trial began when the animal entered the first compartment of the arena from its home cage. The experimenter observed the animal by means of a television monitor in the adjoining room connected to a camera mounted over the arena. The time in seconds to retrieve each successive worm (after the animals crossed the barrier into the second coin, partment) was recorded to the nearest second.

Each animal was given a total of eight trials. The positions of the worms were kept constant on a given trial for all animals and were varied between trials. Two trials/day were given, spaced at least .5 hr apart. After each trial the apparatus was washed to obliterate scent-marking cues. Prior to the series of eight test trials, two preliminary trials were given to familiarize the animals with the task, on these trials five worms were placed in each compartment.

**Results and Discussion**

*Anatomical Results*

The anatomical results are shown in Figure 2 (extent of cortical lesions) and Figure 3 (extent of thalamic degeneration), and it can be seen that the lesions conform in large part to the intended placements. The cortical

lesions in the MT group invaded area MT bilaterally in all cases. One subject (Animal MT-11) also had damage to area 19 on the right hemisphere. As intended, all animals in the XS group had bilateral lesions in area MT, with additional damage to areas 18 and 19. Auditory cortex was invaded in Animals MT-1, MT-11, and XS-6.

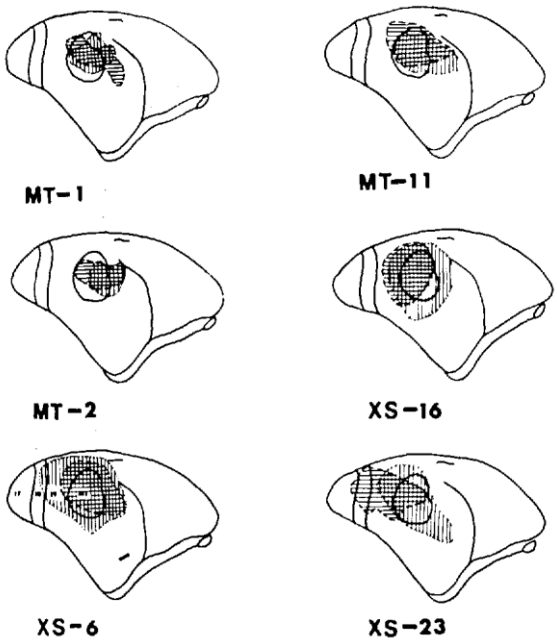



*Figure 2.* Reconstructions of extent of lesions for each animal in the two operated groups. (Lesions in the right hemisphere are shown by horizontal stripes, and lesions in the left hemisphere are shown by vertical stripes. Boundaries between cortical areas 17, 18, 19, and MT are shown by solid lines, based on figures in Glendenning et al., 1975.)

Of the six cases, Animals MT-2 and XS-23 showed the least thalamic degeneration. In both cases there was some bilateral degeneration in the inferior pulvinar, but slight, if any, degeneration in the dorsal lateral geniculate (DGL) nucleus. Cortical damage was confined almost entirely to area MT in Animal MT-2, and in Animal XS-23, area MT and cortex intercalated between 17 and MT were destroyed, with concomitant slight bilateral degeneration in the superior pulvinars and severe degeneration in the left rostral inferior pulvinar.

Three subjects (Animals MT-1, MT-11, and XS-16) showed complete destruction of the tectal pulvinar projection to MT with all or part of the geniculostriate system spared in each case. The inferior pulvinar showed severe degeneration in each case. Some degeneration was also found in the medial geniculate nucleus, the posterior group, and the superior pulvinar.

Animal XS-6 sustained the greatest cortical damage in the operated group. Most of the temporal and occipital lobes was ablated or undercut. The superior and inferior pulvinars contained severe degeneration, as did the dorsal lateral geniculate nuclei. In addition, degeneration was found in the posterior group and medial geniculate nuclei.

Thus, the lesions provide information about the middle temporal area in all six cases, with greater or lesser damage to other extrastriate areas and to the geniculostriate system. A summary of thalamic degeneration in each case is given in Table 1.

Table 1
*Summary of Degeneration in Thalamic Nuclei*

| Animal | Dorsal lateral geniculate | Medial geniculate | Posterior group | Pulvinar inferior | Pulvinar superior |
|---|---|---|---|---|---|
| MT-1 | ++ | ++ | ++ | +++ | + |
| MT-2 | + | 0 | 0 | + | 0 |
| MT-11 | + | ++ | ++ | +++ | 0 |
| XS-6 | +++ | ++ | ++ | +++ | +++ |
| XS-16 | + | 0 | 0 | +++ | ++ |
| XS-23 | 0 | 0 | 0 | + | + |

*Note.* MT = middle temporal; XS = extrastriate plus middle temporal. Severe degeneration, +++; moderate degeneration, ++; slight degeneration, +; no degeneration, 0.

*Visual Discrimination*

After the operated animals had recovered from surgery, all animals were retested on the circular spot problem learned just prior to surgery. Three of the NC animals quickly reached criterion in 30-60 trials. The fourth, Animal NC-10, was balky and difficult to test and required 360 trials to reach criterion.

All the operated animals performed at chance level for several sessions of 30 trials each, and therefore remedial training was given. The partition was removed and larger circles were substituted for the .64-cm circle. Using a titration procedure, we decreased the size of the circle and increased the length of the barrier as the animals reached criterion on each stage of remedial training. Three operated subjects (Animals \S-23, MT-1, and MT-2) eventually mastered the original problem. Animal XS-16 was able to reach criterion on the .64-cm circle with the 15-cm partition, and Animal MT-11 succeeded on a 1.28-cm circle with a partition of 30 cm. Animal XS-6 appeared to have severe visual limitations, and after 800 testing trials, attempts to retrain this animal in the two-choice apparatus were abandoned.

Table 2 shows the percentage correct response to the cue in the first discrimination task, grouped in terms of the distance of the cue from the center of the panel. Results of Animals XS-16 and MT-11 are based on the easier conditions described above. It should be noted that performance did not differ between-the operated and the normal control animals on the eight positions surrounding the center. Nor did performance differ on Positions 9-16. However, when the cue lay in the periphery of the visual display, as in Positions 17-20, the operated animals showed a decrement in performance. Thus, although the overall performance of the groups did not differ, the operated animals showed a selective impairment in locating the cue: Group X Cue interaction, $F(4, 10) = 4.78$, $p = .015$.

Table 2
*Mean Percentage Correct Responses to Stationary and Variable Cues in 20 Locations*

| | Stationary cues | | | Variable cues with partition | | | Variable cues without partition | | |
|---|---|---|---|---|---|---|---|---|---|
| Animal | 1–8 | 9–16 | 17–20 | 1–8 | 9–16 | 17–20 | 1–8 | 9–16 | 17–20 |
| MT-1 | 79 | 82 | 68 | 84 | 82 | 67 | 92 | 84 | 80 |
| MT-2 | 97 | 93 | 84 | 95 | 97 | 87 | 99 | 99 | 100 |
| MT-11 | 92 | 91 | 77 | 86 | 79 | 62 | 96 | 94 | 80 |
| XS-6 | — | — | — | — | — | — | — | — | — |
| XS-16 | 81 | 96 | 75 | 97 | 90 | 75 | 100 | 96 | 90 |
| XS-23 | 91 | 89 | 86 | 95 | 91 | 77 | 100 | 90 | 92 |
| NC-3 | 94 | 92 | 87 | 91 | 92 | 80 | 100 | 99 | 95 |
| NC-4 | 92 | 96 | 90 | 96 | 95 | 90 | 99 | 99 | 87 |
| NC-8 | 74 | 82 | 90 | — | — | — | — | — | — |
| NC-10 | 86 | 92 | 89 | 87 | 85 | 82 | 95 | 95 | 82 |

*Note.* The data are grouped in terms of the distance of the cue from the center of the panel (positions are shown in Figure 1). MT = middle temporal; XS = extrastriate plus middle temporal; NC = normal control.

The success of the operated groups on the warm-up trials and test trials indicates that the observed deficit cannot be attributed to gross sensory impairment or to learning difficulties. However, the question arises as to whether the impairment was due to an inability to execute the appropriate response when the cue was separated by some critical distance from the response and/or reinforcement site. This question can be answered by examining performance on the various peripheral cue positions separately. If the two positions at the top of the stimulus panel (17 and 20) led to poorer performance than the two peripheral positions at the bottom of the stimulus panel (18 and 19), which were closer to the place where the animal responded and retrieved the reward, this would indicate that cue-response separation, rather than the necessity for noticing peripherally presented information, was the critical factor.

Table 3 shows levels of performance for each animal at the cue locations at the top and bottom of the stimulus plaque. It can be seen that there is no consistent pattern relating successful performance and cue- response separation. Three of the operated subjects (Animals XS-16, XS-23, and MT-2) actually performed more poorly with peripheral cues that were contiguous with the response site. The results of the first visual discrimination task suggest, therefore, that extrastriate lesions including area MT lead to an inability to attend to information specifying a target location in the visual field which lies removed from a previously learned fixation point and that this impairment is independent of acuity deficits, learning disability, or inability to associate a spatially discontiguous cue and response. The animals with more complete ablations of the pulvinar-MT pathway (Animals MT-1, MT-11, and XS-16) were most severely impaired, but all animals with lesions were affected to some extent.

Table 2 shows percentage correct response for the three groups on the discrimination tasks in which the cue varied in location from trial to trial. Animal MT-11 succeeded in reaching criterion on warm-up trials on the .64-cm spot with the 30-cm partition, and test trials were therefore given under these conditions for this animal. Results for the NC group are based on three subjects since Animal NC-8 died during testing.

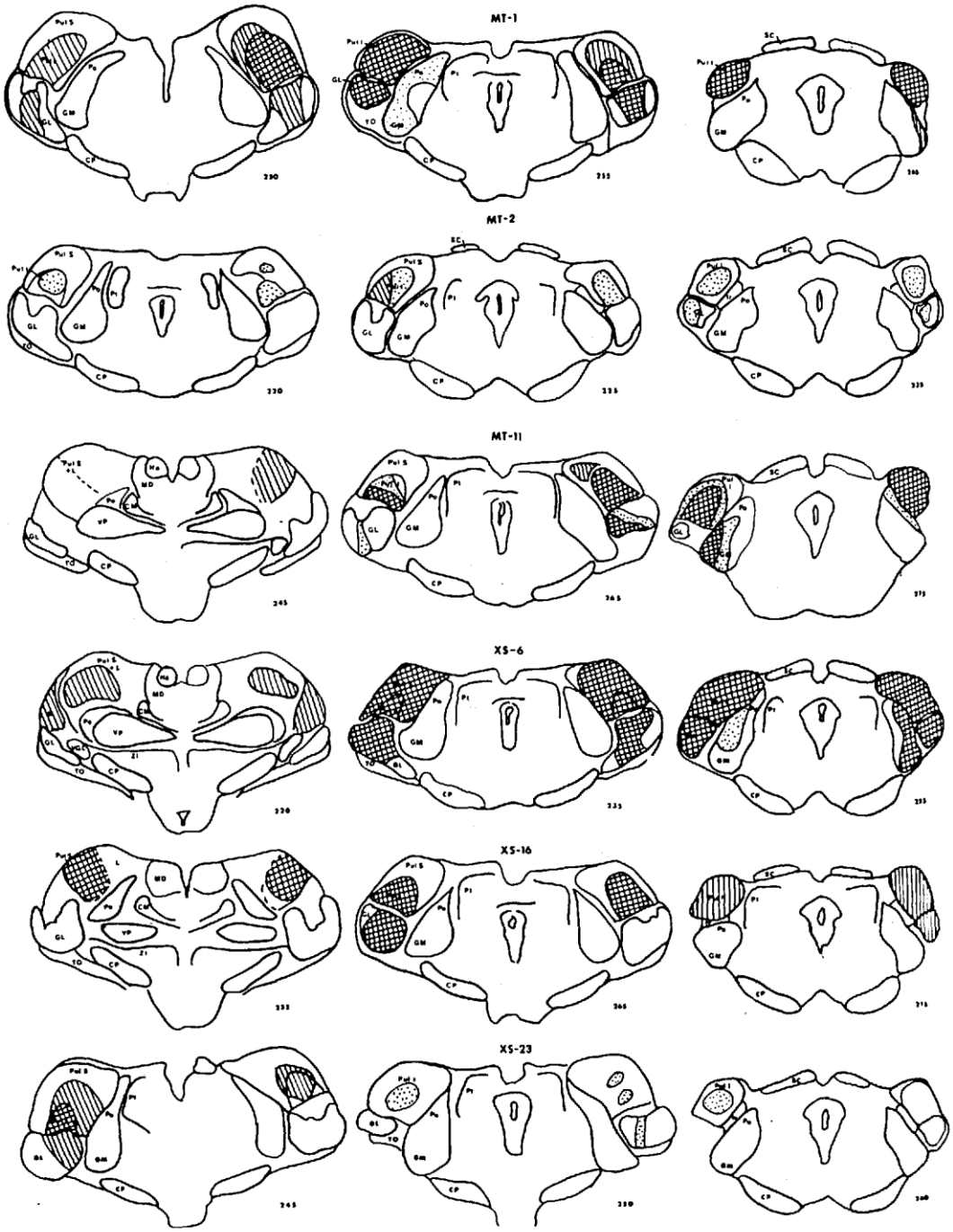



*Figure 3.* Reconstructions of extent of thalamic degeneration for each animal in the two operated groups. (Severe degeneration shown by cross-hatching, moderate degeneration by stripes, and slight degeneration by stippling.)

When the partition was removed, there was no difference between the groups, and performance improved for all animals. This was perhaps due to the fact that the animals were not committed to a choice until they pushed the stimulus panel, but since this was the last series of trials given, the improvement may also have been due to practice.

Table 3
*Percentage Correct Responses on Visual Discrimination Task With Stationary Stimuli*

| Animal | Cues on top of plaque | Cues on bottom of plaque |
|---|---|---|
| MT-1 | 58.5 | 78.0 |
| MT-2 | 90.0 | 78.5 |
| MT-11 | 73.0 | 82.0 |
| XS-6 | — | — |
| XS-16 | 85.0 | 65.0 |
| XS-23 | 96.5 | 75.0 |
| NC-3 | 87.0 | 88.5 |
| NC-4 | 98.5 | 82.5 |
| NC-8 | 90.0 | 88.5 |
| NC-10 | 86.5 | 93.5 |

*Note.* MT = middle temporal; XS = extrastriate plus middle temporal; NC = normal control.

However, with the barrier present, all groups performed relatively less well with peripherally located cues, and the performance decrement was greater for the operated animals than for the normal control animals: Group X Cue interaction, $F(4, 10) = 3{,}78$, $p = .04$.

These data confirm the results of the first visual discrimination test in showing that destruction of the pulvinar/extrastriate pathway affects the capacity of the animal to use cues in visual space effectively, Here, the task demanded scanning some or allot the whole visual array on every trial, since , the position of the cue varied from trial to trial in an unpredictable manner. Again, it was found that for the animals with greater degeneration in the inferior pulvinar (Animals MT-1, MT-11, and XS-16), cues farther removed from the point that they had previously learned to look at were noticed less easily than those closer to it. The ablation of additional cortical visual areas outside of area MT did not greatly exacerbate the deficit.

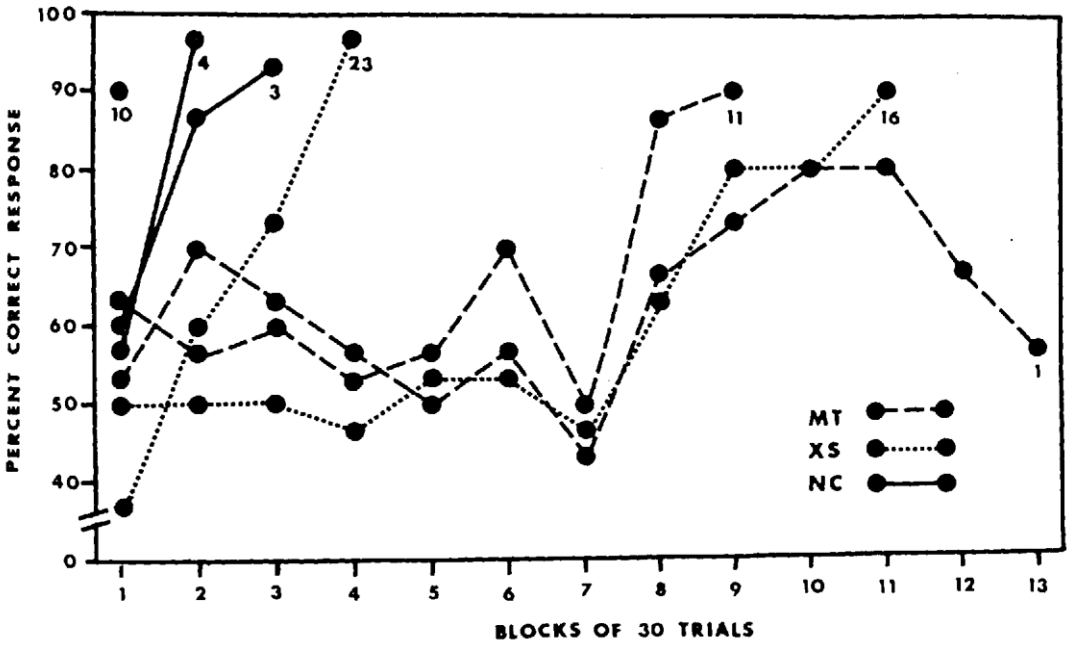



*Figure 4.* Individual learning curves for animals tested on horizontal-vertical stripe discrimination.

The results of the horizontal-vertical-pattern discrimination learning test are shown in Figure 4. The subject with the largest lesion (Animal XS-6) still appeared to be unable to use visual cues, and formal testing was not attempted. There are no results for Animal MT-2, which was sacrificed before this test was completed, so the

data represent four animals with lesions and three NC animals. The number of 30-trial sessions to criterion and the percentage of , correct responses on each block of 30 trials are shown for individual animals. The three NC animals learned the task quickly; the four operated animals were retarded. However, Animal XS-23 showed an essentially normal learning curve, given its initial preference for the negative stimulus. Testing was discontinued for Animal MT-1 because of its inability to learn the problem in 400 trials. A Mann-Whitney test showed that the difference between the combined lesion groups and the NC group is significant ($U = 0$, $p = .028$), but the fact that three of the operated animals were able to reach criterion on the discrimination task in the time allotted argues against a profound sensory loss.

*Spatial Localization*

Figure 5 shows the median number of seconds each animal took on the H, V, and H-V pathways. The performance of all subjects except Animal XS-6 was similar on the warm-up trials, which required merely running straight through the tunnel on the floor. In contrast to the others, Animal XS-6 failed all the problems presented and did not demonstrate the upright orientation posture commonly seen in the other animals as they looked about the tunnel. Because of its consistent failure under all conditions and its apparent inability to use visual cues at all, testing was discontinued for this animal after 21 trials.

The XS group failed more trials than the MT group, which in turn performed worse than the NC group. The difference in overall performance of the groups was significant, $F(2, 6) = 9.42$, $p = .01$. However, it is also clear that there are no consistent differences in the performance of the operated and normal animals on the horizontal pathways, and only on the V and H-V pathways were the operated animals impaired. There is a common feature of the pathways on which the operated animals had the greatest difficulty: The short and long V pathways and the short H-V pathway required the animal to jump to a hole in the center of the partition (cf. Figure 5). With more experience, Animals MT-2 and MT-11 eventually succeeded on some trials. Animals with damage to the superior pulvinar system (Animal MT-1 and the XS group) were consistently unable to get through the tunnel under this condition. In addition, these animals had difficulty on H-V pathways without center holes. In contrast to the operated animals, the NC animals showed no difficulty in traversing the tunnel under any condition, although their performance was best on H pathways.

Television monitoring of the animals' performance revealed that they used different strategies in getting through the tunnel. The NC animals ran, climbed, or jumped directly from hole to hole, spending little time on the tunnel floor. Some of the animals with lesions climbed the wire mesh walls and ceiling to reach holes off the floor, and they often made unsuccessful attempts to reach a center hole. Occasionally they attempted to jump to a center hole from the floor or sides of the tunnel, but the majority of jumps were unsuccessful. Animal MT-11 appeared to jump accurately in terms of direction but reached the apex of the leap approximately 1/3 m short of the opening. At this point, it extended its limbs but rarely succeeded in grabbing the ledge of the hole, and it usually fell to the floor. Animal MT-2 initially jumped with sufficient force to hit its head on the partition next to the opening, extending its limbs in a fashion similar to that of Animal MT-11, before falling to the floor. Over trials, the topography and accuracy of this animal's jumps became more precise until by the end of testing, it was indistinguishable from the NC animals. Animal MT-1 attempted to climb and jump to holes off the floor but did not succeed.

The animals with larger lesions were more profoundly impaired. Animal XS-6 failed all trials. Animals XS-16 and XS-23 never succeeded in reaching a center hole, and their behavior was unusual on all trials. These animals initially ran slowly along the walls of the tunnel, occasionally running into a wall before finding the holes on the H pathway. Their behavior was also unusual in that they exhibited a low crouching behavior typical of bushbabies in the wild when they climb through dense foliage, and they never engaged in the short hops and longer stereotyped jumps that are typical of bush- babies when they leave their aboreal habitats for the ground (Doyle, 1974). Furthermore, the animals with the larger lesions were never seen to jump to a wall or partition in the tunnel.

MEDIAN NUMBER OF SECONDS TO TRAVERSE TUNNEL

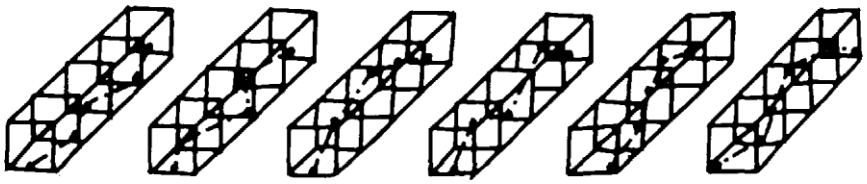
| GROUP | TYPE OF PATHWAY | | | | | |
|---|---|---|---|---|---|---|
| | HORIZONTAL | | VERTICAL | | HORIZONTAL–VERTICAL | |
| | S | L | S | L | S | L |
|  | | | | | | |
| MT | | | | | | |
| 1 | 73 (0) | 190 (4) | F (9) | F (9) | F (9) | F (9) |
| 2 | 36 (0) | 31 (0) | F (8) | 73 (4) | 79 (4) | 79 (0) |
| 11 | 30 (0) | 38 (1) | F (7) | F (6) | F (7) | 129 (2) |
| XS | | | | | | |
| 6 | F (4/4) | F (4/4) | F (4/4) | F (4/4) | F (3/3) | F (2/2) |
| 16 | 84 (0) | 80 (0) | F (9) | F (9) | F (9) | F (7) |
| 23 | 55 (2) | 88 (0) | F (9) | F (9) | F (9) | F (5) |
| NC | | | | | | |
| 3 | 39 (0) | 42 (1) | 74 (0) | 76 (1) | 57 (0) | 79 (0) |
| 4 | 86 (0) | 94 (0) | 147 (0) | 160 (0) | 134 (0) | 224 (0) |
| 10 | 60 (1) | 53 (1) | 124 (3) | 83 (2) | 86 (2) | 130 (2) |

*Figure 5.* Results of test requiring animals to find various pathways through holes in barriers. (Typical arrangements are shown for each of the six conditions described in the text. Horizontal pathways did not require the animal to leave the floor. Vertical pathways did not require the animal to look from side to side. Horizontal-vertical pathways required both. The letter S indicates a shorter pathway through the tunnel, and L indicates a longer pathway. The numbers in parenthesis indicate the number of times an animal failed to traverse the tunnel within 600 sec. Trials were terminated for XS-6 because of consistent failure under all conditions.)

*Ambient Visual Search*

Results for the arena test are based on scores for five operated subjects, including Animal XS-6, and three normal controls. The mean time in seconds taken to find each successive worm based on eight trials is shown in Figure 6. The scores represent the time from crossing the barrier separating the two compartments to time of retrieval of the first worm, time to locate the second worm after the first worm had been retrieved, and so on. The animals with XS lesions were slower than the animals with MT lesions, and both groups were slower than the NC group, $F(2, 5) = 11.18$, $p = .01$. This impairment became more pronounced as successive worms were retrieved. Indeed, the first few worms were quickly noticed by all animals, and only as more visual search was required did the difference between normal and operated animals become marked, $F(10, 25) = 4.44$, $p = .001$.

The arena test, while simple, is perhaps the purest indicator of an animal's ability to locate meaningful information in space. It is worth noting that it was the only task that Animal XS-6 was able to perform. The test required no formal training and no differential choices. It is certain that all the animals could identify the stimuli and were motivated to do so. Thus, these results support the findings from the more formal tests which indicated similar deficits in visually guided behavior on the part of operated animals.

**General Discussion**

The patterns of behavioral results that were obtained can be related to damage to the three ascending thalamocortical pathways in the bushbaby. Destruction of area MT appears to be a sufficient condition for producing a deficit in visual search if this is defined as the process of acquiring a target in visual space that can be used to guide behavior appropriately. All operated animals had degeneration in the inferior pulvinar nucleus, and all were impaired on the tasks requiring visuospatial localization. The fact that animals with MT lesions were impaired in reaching the target in the tunnel apparatus only when the target was in the center of the partition appears to be inconsistent with the impairment in utilizing visual cues in the peripheral field, which was observed in the discrimination apparatus. The fact that MT lesions produced deficits in these different aspects of visuospatial behavior leads to the suggestion that explicit visual search may not be the underlying factor in their impairment. Rather, it may be a difficulty in achieving and maintaining fixation on a target, which was not previously the focus of attention, that underlies the deficits. The fact that these animals looked about the compartments and attempted to jump to the center hole in the tunnel apparatus suggests that some visual search had taken place but that the information was not adequate for guiding behavior.

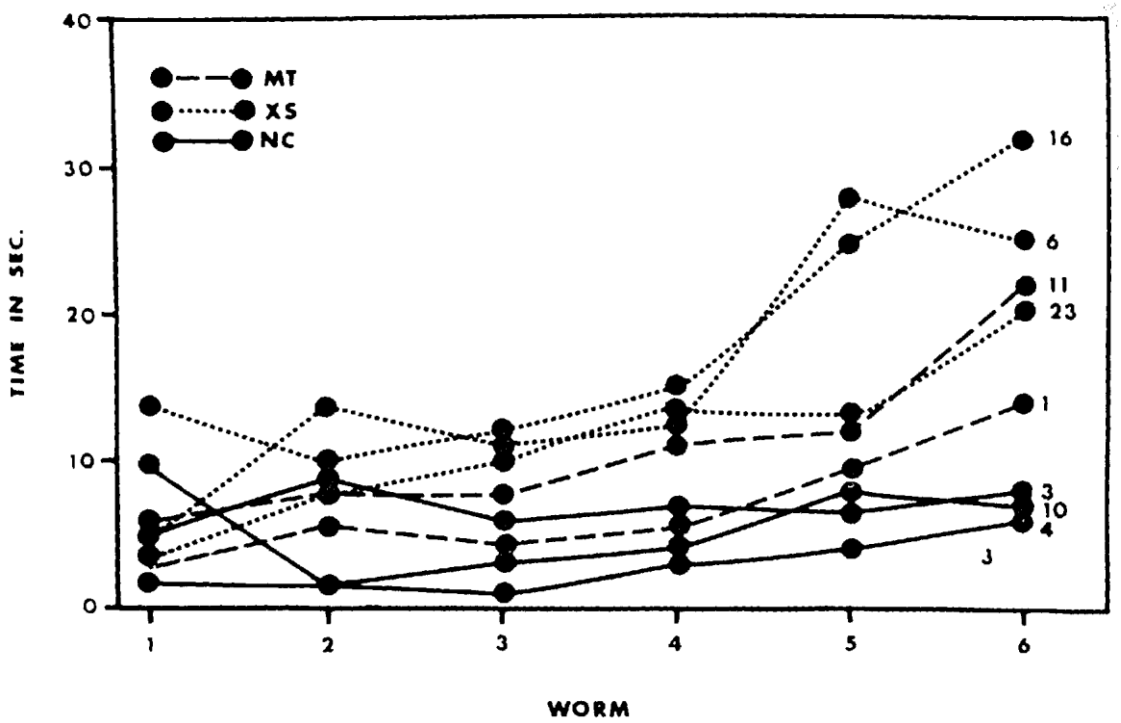



*Figure 6.* The number of seconds to find each successive worm in the arena is shown for each animal. (The scores represent the time taken to find the first worm, the time between finding the second worm after the first worm had been located, and so on.)

While damage to the tectal-pulvinar pathway was sufficient to produce an impairment in visuospatial localization, animals with larger extrastriate lesions and greater damage to the superior pulvinarextrastriate pathway were more severely impaired. These animals had difficulty in traversing a pathway through the tunnel even when jumping to a center hole was not required. They also were observed engaging in wall-hugging behavior, and they rarely looked or jumped about the compartments. This behavior suggests a more general disorientation in space as well as an inability to maintain the spatial coordinates of a target. Locating a food object in space also proved more difficult for the XS group, although all operated animals performed worse than NC animals. To succeed on the tunnel and ambient search tasks, the animal had to use information specifying the location of a target to direct its behavior to that particular location in space. These results lead to the hypothesis that areas 18 and 19 are important in elaborating a visuospatial framework whereas area MT serves to maintain fixation on a relevant point within that framework (MacKay, 1973).

It should be noted that animals in both operated groups were able to identify and locate the .64-cm spot that served as the cue in the discrimination apparatus and that always appeared in the center of the stimuli's plaque

in warm-up trials. The variability of spatial information in the cue location and tunnel tasks appears to be a critical variable in producing the impairment.

Although all operated animals tested were slower than NC animals in learning the stripe orientation task, it can be concluded that the results were due to interruption of the optic radiations. The most retarded subject (Animal MT-1) had the most degeneration in the lateral geniculate nucleus, and the one with an essentially normal learning curve (Animal XS-23) had little or no damage to the DGL. It can be concluded that area MT and areas 18 and 19 are not necessary for simple discrimination learning when locating information in space is not a critical factor in performance. Conversely, damage to the geniculostriate system was not necessary to produce the visuospatial impairments discussed.

As noted above, a cortical area in rhesus monkey, which may be homologous to area MT in the bushbaby, is found in the posterior bank of the superior temporal sulcus (Zeki, 1974). This area has also been implicated in visual search processes by Wilson et al. (1977), and there may be an area that serves similar behavioral functions in all primates. It is more difficult to establish homologies to areas 18 and 19 in the bush- baby since thalamic input to these areas in rhesus monkey is derived from both tectorecipient and nontectorecipient portions of the pulvinar. However, there are data that point to the importance of prestriate cortex in the rhesus monkey in visuospatial function (Bates & Ettlinger, 1960; Pohl, 1973; Wilson, 1957). Prestriate cortex in the bushbaby as well as in the monkey may serve to establish a spatial frame of reference within which visual search and fixation can be accomplished.

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